Vol. 412: 223–230, 2010
doi: 10.3354/meps08676

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published August 18

Panmictic population structure in the migratory marine sparid *Acanthopagrus australis* despite its close association with estuaries

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ABSTRACT: Recent studies have revealed surprising levels of genetic structuring within populations of marine species that were previously thought to be widely dispersed. Such subdivision may reflect unexpected physical or biological barriers to dispersal, including philopatric behaviour. Here we investigate the genetic structure of the eastern Australian yellowfin bream *Acanthopagrus australis*—a widely distributed species that is thought to be highly dispersive but is also known to spawn in close association with estuaries. Our data from surveys of allele frequencies at 6 microsatellite DNA loci for 350 fish revealed high levels of genetic diversity within all sites but no genetic differentiation of groups of recruits collected from sites separated by a distance of up to 50 km (allele frequency differentiation: F_{ST} = 0.002, p > 0.05). Moreover, there was no differentiation of adults spread across the distributional range of the species (several 100s of kilometers, F_{ST} = 0.002). We conclude that *A. australis* spawning is opportunistically associated with estuaries in general, and that the species essentially forms a panmictic population with a genetic homogeneity reflecting the predicted active northwards dispersal of adults and the southwards dispersal of larvae as affected by the Eastern Australian Current.

KEY WORDS: Dispersal · Gene flow · East Australian Current · Microsatellites · Sparidae · Coastal lake or lagoon · Yellowfin bream

INTRODUCTION

Mobile marine organisms such as fish may be expected to form large populations that are strongly interconnected by dispersal, and hence display little genetic subdivision. However, recent studies have highlighted both the surprisingly restricted dispersal of many marine taxa (Jones et al. 1999, Almany et al. 2007) and the consequent high level of population subdivision even within taxa with long-lived larvae or mobile adults (Ayre & Dufty 1994). Many factors, including ocean currents (James et al. 2002), coastal features such as estuaries or embayments (Watts & Johnson 2004), and complex larval and/or adult behaviour (Gerlach et al. 2007, Dixson et al. 2008), have been implicated. Hence, predictions that the life history of fish should result in widespread dispersal must always be treated with caution.

A diverse range of marine animals displays spawning site fidelity (e.g. sea kraits, Shetty & Shine 2002; turtles, Bowen et al. 2005, groupers, Starr et al. 2007). This trait is common in many groups of fish and may involve the adults returning to their place of birth to spawn (i.e. natal-site spawning) (e.g. Thorrold et al. 2001). Although the exact mechanism facilitating spawning site faithfulness is often unclear, it seems probable that it relies on individuals sensing and 'homing' to some underlying characteristic or environmental factor associated with the spawning site. For example, the navigational mechanism facilitating natal-site spawning in estuarine (i.e. stream or river) dependent salmon is thought to involve olfactory imprinting (dur-

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ing early life stages), and subsequent sensing of natal-site odours (Dittman & Quinn 1996, Yamamoto et al. 2010).

On the east coast of Australia, *Acanthopagrus australis* Günther (yellowfin bream) is considered to be highly mobile and is treated as a single (fisheries) stock ranging over >2000 km from southern Queensland (QLD) to the New South Wales (NSW)/Victoria (VIC) state border (Henry & Lyle 2003). Indeed, 2 studies have shown bream (which the authors assumed were *A. australis* rather than the estuary restricted congener *A. butcheri* Munro (black bream) that were tagged within both central and northern NSW estuaries being recaptured in locations in southern Queensland (Henry 1983, West 1993). While these tagging studies clearly show that a small proportion of *A. australis* undertake long-distance migration (in a southerly direction, ranging over 10s to 100s of kilometres) (proportion of the total no. of fish that emigrated to the total no. of fish tagged and released: 29/589, 12 588 [total no. of fish tagged], West 1993; 4/88, 1058 [total no. of fish tagged], Henry 1983), both authors reported that the majority of recaptured fish were caught within the estuary in which they were tagged (560/589 and 84/88 respectively). These findings support earlier work by Pollock (1982a), who similarly used capture-tag-release-recapture data to show that *A. australis* inhabiting Moreton Bay (QLD) at approximately the northern range limit of the species should be considered as a separate (fisheries) stock, as fish did not emigrate outside of Moreton Bay. Taken at face value, these findings, together with aspects of the life history of *A. australis*, suggest that populations could be genetically subdivided.

Although adult *Acanthopagrus australis* are thought to migrate in a southerly direction to spawn, and pelagic larvae are thought to be dispersed over large distances by the East Australian Current (EAC), the species may display spawning site fidelity. Spawning behaviour is relatively unstudied in *A. australis*, although spawning is thought to occur in entrance channels or lower reaches of coastal lakes and lagoons ('estuaries') or in the surf zone of beaches adjacent to the entrances of estuaries (Pollock 1982b, 1984). This close association with estuarine spawning sites has the potential to promote fine-scale genetic differentiation of both adult and juvenile populations if *A. australis* lineages maintain prolonged associations with individual estuaries. Alternatively, if spawning is simply opportunistically associated with estuaries in general, and larvae are mixed and transported over a wide area by the EAC, then we would expect little or no population subdivision.

Here we use population genetic data to test the prediction that spawning site fidelity promotes fine-scale population subdivision in *Acanthopagrus australis*. Specifically, we compare the degree of genetic differentiation of sets of *A. australis* recruits within different estuaries with that of adults caught near estuaries but on the open coast.

MATERIALS AND METHODS

The *Acanthopagrus* species complex, sample collections, and genetic markers. *A. australis* is distributed continuously along the east coast of Australia from southern QLD to approximately the NSW/VIC state border (Fig. 1) (Edgar 2000). It inhabits a range of habitats encompassing rocky headlands, offshore reefs and the surf zone of coastal beaches as well as estuaries. The species has an annual reproductive cycle, with asynchronous gonad development and group spawning occurring over a period of 2 to 5 mo. Peak spawning occurs between April and June (on

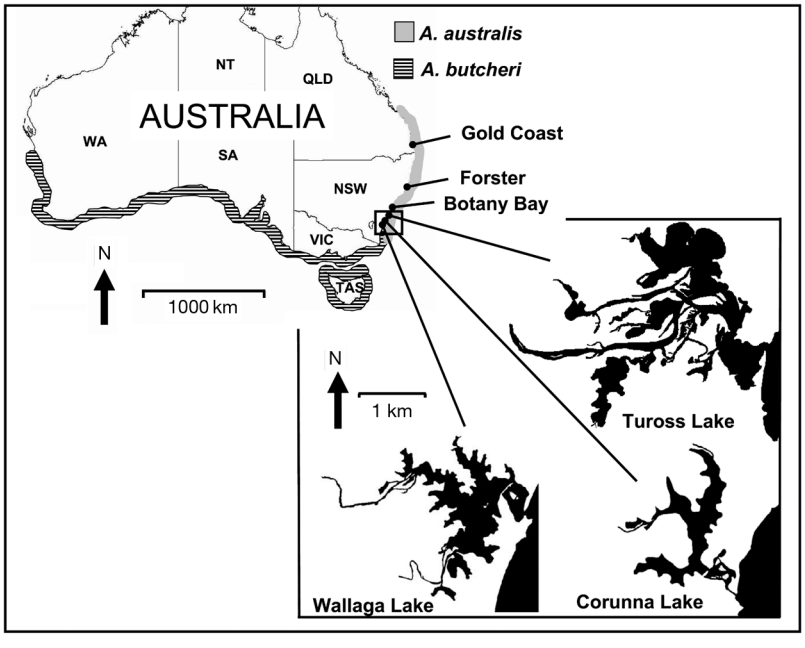

Fig. 1. Distribution of *Acanthopagrus australis* and its estuary restricted congener *A. butcheri*, and the locations of sampling sites for juvenile (Tuross, Corunna and Wallaga Lakes) and adult (Gold Coast, Forster and Botany Bay) *A. australis*

the north coast but may be later on the south coast, i.e. July/August, C. A. Gray pers. comm.). During the spawning period, an unknown proportion of the population is thought to migrate in a southerly direction along the coast, with fish forming large aggregations in the lower reaches of estuaries and/or in the immediate surf zone of coastal beaches directly adjacent to the entrances of estuaries, presumably to spawn (Pollock 1982b, 1984). Larvae may be dispersed over a wide area as they are thought to spend a large amount of time in the coastal ocean plankton under the influence of the East Australian Current (EAC) while undergoing development (Neira et al. 1998) before recruiting to shallow seagrass meadows and submerged structures in coastal lakes and lagoons (Griffiths 2001).

The dispersal potential of *Acanthopagrus australis* could have serious implications for its estuary restricted congener, *A. butcheri*. This is because on the southeast corner of Australia where the 2 species co-occur within estuaries, *A. australis* has made a major contribution to the genotypes of *A. butcheri* through hybridisation and introgression (Rowland 1984, Roberts et al. 2009). The juvenile *A. australis* examined in this study represent a subset of a collection of *Acanthopagrus* spp. from Roberts et al. (2010), who determined the proportion of *A. australis*, *A. butcheri* and introgressed or hybrid bream within 5 coastal lagoons in southern NSW. Roberts et al. (2010) collected 688 juvenile (<30 mm length) *Acanthopagrus* spp. (81 to 170 per lagoon) following a single recruitment event in 2002, after the 2001 spawning. Between 20 and 66 bream were sampled at each of 3 or 4 haphazardly chosen sites (within seagrass meadows) in each lagoon. Bream were captured with a 10 × 2 m haul seine net (6 mm mesh) over a ~25 m^2 area. The species specific status of every individual was determined using admixture analysis based on 8 microsatellite loci, and a species specific mtDNA RFLP (restriction fragment length polymorphism) profile (Roberts et al. 2010). The microsatellite markers and the PCR cycling conditions are described in Roberts et al. (2009).

We examined microsatellite genotypes for 30 randomly selected juvenile *Acanthopagrus australis* from 2 or 3 sites, within each of 3 lagoons on the NSW south coast (Tuross, Corunna and Wallaga Lakes) separated by a distance of up to 50 km (total n = 240 fish). We also genotyped sets of ocean-caught adults from each of 3 locations: the Gold Coast (QLD) (n = 40), Forster (n = 40) and Botany Bay (n = 30) (NSW) (total n = 110) (Fig. 1). These fish were included to compare the genetic similarity of juvenile bream on the south coast of NSW to adult bream from throughout the described range of the species.

Genetic analyses: microsatellites. For each site within a lagoon, and for each ocean location, we calculated the average number of alleles per locus, and the average observed and expected heterozygosity (using POPGENE; Yeh et al. 1999).

Because incorrect interpretation of microsatellite data can occur when there are genotyping errors associated with null alleles, stutter bands due to replication slippage during PCR, and/or large allele dropout, we determined whether our data were affected by these potential sources of error using the program Micro Checker (van Oosterhout et al. 2004). Separate analyses on the overall collection of juveniles and adults for each lagoon and ocean site revealed that 2 loci (*pAb2A5* and *Acs3**) had apparent large excesses of homozygotes consistent with null alleles. Although a small number of controlled crosses involving *Acanthopagrus butcheri* × *A. butcheri*, and *A. australis* × *A. butcheri* have revealed simple Mendelian inheritance and no evidence of null alleles for the 8 microsatellite loci (4 pairs; 30 larvae per pair) (Roberts et al. 2009), we have opted to present the results here based on just 6 loci, acknowledging the possibility of null alleles at *pAb2A5* and *Acs3** in *A. australis*.

We estimated Weir & Cockerham's (1984) formulations of Wright's (1969) *F*-statistics using the program Tools for Population Genetic Analyses (TFPGA; Miller 1997). Our hierarchical sampling of juveniles within south coast lagoons allowed us to partition genetic variation into separate variance components. In the present study, the hierarchical levels in the data were denoted by F_{SL} and F_{LT}, which respectively represent genetic differentiation among sites within a specified lagoon, and among lagoons relative to the total. F_{IS} and F_{IT} are measures of the deviation from Hardy-Weinberg expectations within subpopulations (i.e. lagoons) and in the total population (sample) respectively, and are presented in the conventional way. The estimates were based on microsatellite allele frequencies for individual loci, and as an average across loci. Bootstrapping and jackknifing over loci were used to estimate SDs and 95% CIs. *F*-statistics were considered statistically significant when the lower 95% CI did not overlap 0. Comparable *F*-statistics for ocean-caught adults were also included, although our sampling did not permit a hierarchical assessment of population differentiation. We tested for differentiation of adult and juvenile *Acanthopagrus australis* by calculating F_{ST} (i.e. allele frequency differentiation among subpopulations) for the overall sets of adult and juvenile fish. Finally, to visually display any geographic structuring within our microsatellite data set, we performed factorial correspondence analysis (FCA) in GENETIX 4.03 (Belkhir et al. 2002) on the pooled sample of juveniles from each lagoon together with the sample of ocean-caught adults.

Table 1. *Acanthopagrus australis*. Mean (±SE) number of alleles (*A*), number of private alleles (alleles unique to a particular site) (A_P), observed heterozygosity (H_o), Nei's 1973 expected heterozygosity (H_e), and the estimator *f* of the inbreeding coefficient, F_{IS} (Weir & Cockerham 1984) based on 6 microsatellite loci, for juveniles (representing the same year of birth) in 3 coastal lagoons in southeastern Australia. Sample size was 30 fish per site. *Statistically significant departure from Hardy-Weinberg equilibria, $p < 0.05$

	Tuross			Corunna			Wallaga	
	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3	Site 1	Site 2
A	11.3 (1.9)	11.8 (2.1)	11.5 (2.6)	11.8 (2.3)	11.7 (2.0)	11.3 (1.7)	11.7 (2.2)	13.0 (1.8)
A_P	0.33 (0.21)	0.50 (0.22)	0.00 (0.00)	0.17 (0.17)	0.50 (0.22)	0.50 (0.22)	0.00 (0.00)	0.67 (0.21)
H_o	0.833 (0.092)	0.788 (0.107)	0.806 (0.184)	0.778 (0.136)	0.759 (0.090)	0.817 (0.089)	0.811 (0.103)	0.783 (0.161)
H_e	0.813 (0.083)	0.790 (0.104)	0.783 (0.133)	0.790 (0.123)	0.801 (0.106)	0.812 (0.099)	0.796 (0.112)	0.807 (0.120)
f	−0.009	0.020	−0.011	0.031	0.076*	0.011	−0.002	0.047*

Table 2. *Acanthopagrus australis*. Hierarchical *F*-statistics estimated for 6 microsatellite loci, and overall, for juveniles within 3 coastal lagoons. F_{SL} and F_{LT}: genetic differentiation among sites within lagoons, and among lagoons respectively. F_{IS} and F_{IT}: degree of deviation from Hardy-Weinberg expectations within lagoons and within the total sample. *F*-statistics were considered statistically significant when the lower 95% CI did not overlap 0

Locus	F_{IS}	F_{SL}	F_{LT}	F_{IT}
pAb2B7	0.045	0.004	0.003	0.049
pAb2D1	−0.020	0.002	−0.002	−0.018
*Acs1**	0.031	0.006	0.011	0.037
*Acs6**	0.033	−0.005	0.004	0.028
*Acs-16**	0.014	0.001	−0.001	0.015
*Acs-21**	0.013	−0.001	−0.004	0.012
Overall ± SD	0.021 ± 0.008	0.001 ± 0.002	0.002 ± 0.002	0.022 ± 0.009
95% CI	0.004 – 0.008	−0.001 – 0.004	−0.002 – 0.006	0.004 – 0.037

RESULTS

The overall collection of juvenile *Acanthopagrus australis* comprised a genetically diverse group with little evidence of genetic subdivision. Numbers of alleles per locus ranged between 9 and 30, with an average (±SE) of 17.7 (±3.0). We detected similar levels of genetic variation at all sites within each lagoon. The mean number of alleles per locus ranged between 11.3 and 13.0, while mean observed heterozygosity was >0.75 for each site (range: 0.76–0.83). Between 64.2 and 73.6% of all alleles were present at each site. Private alleles (alleles unique to a single site) were extremely rare (16/106 alleles detected), and were found at low frequency (<0.05) when they occurred. Private alleles were distributed evenly among sites within lagoons (Table 1).

Our estimates of genetic variation among sites within lagoons (F_{SL}: 0.001 ± 0.002) and among lagoons (F_{LT}: 0.002 ± 0.002) were extremely low and not significantly different from 0 (based on 95% CIs), indicating no genetic subdivision at either spatial scale. Our estimates of F_{IS} and F_{IT} were also consistently close to 0 (0.021 ± 0.008 and 0.022 ± 0.009 respectively), which together with the lack of spatial variation in allele frequencies, imply a single outcrossed population (Table 2).

Genetic diversity in ocean-caught adults on the north coast was comparable to levels of genetic diversity in the set of juveniles within lagoons on the south coast. The mean number of alleles per locus ranged between 11.5 and 12.2, while mean observed heterozygosity was similarly ≥0.75 for each location (Table 3).

There was no population differentiation among samples of ocean-caught *Acanthopagrus australis* from locations that were spread across the described range of the species (F_{ST} = 0.002 ± 0.001; 95% CI = 0.000–0.004) (Table 4). Perhaps not surprisingly, the FCA plot that was used to compare the genetic simila-

Table 3. *Acanthopagrus australis*. Mean (±SE) number of alleles (*A*), number of private alleles (alleles unique to a particular location) (A_P), observed heterozygosity (H_o) and Nei's 1973 expected heterozygosity (H_e) based on 6 microsatellite loci, for ocean-caught adults. Sample size per location was 40, 40 and 30 fish, respectively

	Gold Coast	Forster	Botany Bay
A	12.2 (2.1)	12.0 (2.6)	11.5 (2.7)
A_P	1.5 (0.3)	1.5 (0.7)	1.0 (0.4)
H_o	0.748 (0.061)	0.771 (0.037)	0.787 (0.051)
H_e	0.800 (0.048)	0.789 (0.054)	0.800 (0.048)

Table 4. *Acanthopagrus australis*. *F*-statistics estimated for 6 microsatellite loci, and overall, for ocean-caught adults, and for the pooled set of juvenile (estuarine) and adult fish. F_{IS} and F_{IT}: degree of deviation from Hardy-Weinberg expectations within lagoons and within the total sample; F_{ST}: allele frequency differentiation among subpopulations (i.e. sampling locations)

Locus	Adult			Adult & juvenile		
	F_{IS}	F_{ST}	F_{IT}	F_{IS}	F_{ST}	F_{IT}
pAb2B7	0.085	−0.005	0.085	0.059	−0.001	0.059
pAb2D1	0.034	0.005	0.039	−0.001	0.001	−0.001
*Acs1**	0.059	0.000	0.059	0.041	−0.003	0.039
*Acs6**	0.034	0.005	0.039	0.031	−0.001	0.030
*Acs-16**	0.035	0.001	0.036	0.021	0.001	0.022
*Acs-21**	0.024	0.001	0.026	0.017	−0.001	0.016
Overall ± SD	0.046 ± 0.010	0.002 ± 0.001	0.047 ± 0.010	0.029 ± 0.008	−0.001 ± 0.001	0.029 ± 0.008
95% CI	0.031 – 0.066	0.000 – 0.004	0.033 – 0.066	0.015 – 0.045	−0.002 – 0.001	0.015 – 0.044

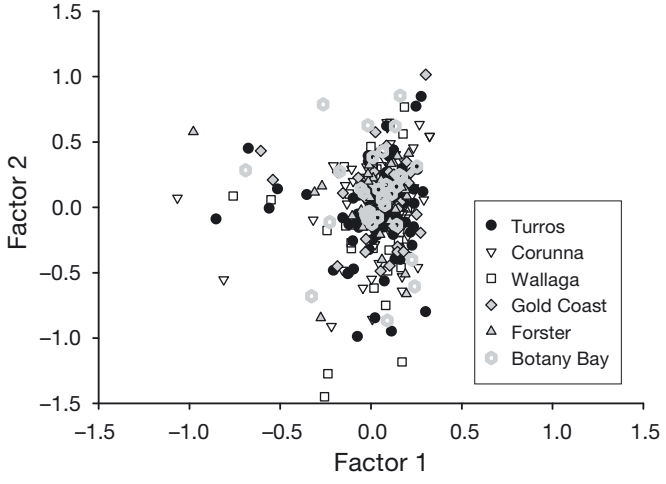

Fig. 2. *Acanthopagrus australis*. Factorial correspondence analysis based on the 6 locus genotype of all 350 fish. $n_{juveniles}$ = 240 (Tuross, Corunna and Wallaga); n_{adults} = 110 (Gold Coast, Forster and Botany Bay). Juveniles were caught within coastal lagoons, while adults represent ocean-caught fish

rity of individual juveniles within lagoons on the south coast to that of ocean-caught adults on the north coast revealed a wide scatter of points along both axes but with the plotted positions of points for the juveniles and adults overlapping (Fig. 2). No sets of juveniles or adults formed clusters of individuals from the same sampling location. Moreover, F_{ST} based on comparison of the overall data set of adult and juvenile fish revealed no genetic differentiation (F_{ST} = 0.000) (Table 4).

DISCUSSION

Our findings suggest that *Acanthopagrus australis* forms a genetically diverse and homogeneous population despite the potential for population subdivision suggested by its close association with estuaries. These results are consistent with the great mobility of this species that has been predicted from tagging studies (Henry 1983, West 1993), and imply that fish have no persistent associations with their natal spawning sites or nursery estuaries. Indeed, all estuarine populations were genotypically diverse and genetically homogenous over spatial scales ranging from several hundreds of meters to tens of kilometres. Estuaries can provide unique opportunities for divergence (see Watts & Johnson 2004 for review), and there are examples where species of fish that are otherwise 'good dispersers' (i.e. mobile adults, with dispersive pelagic larvae) exist as estuary associated, genetically subdivided populations (Johnson et al. 1986, Gold et al. 1999). Our data show that dispersal is clearly sufficient to prevent geographic differentiation of *A. australis* populations despite the acknowledged association of adult *A. australis* with estuaries as feeding and spawning sites. However, this need not imply vast amounts of migration, but simply enough migration to homogenise allele frequencies (Wright 1931). The lack of genetic heterogeneity in *A. australis* among estuaries sharply contrasts with the pattern of genetic subdivision that has been reported for its estuary restricted congener, *A. butcheri*, in at least some parts of its range (Chaplin et al. 1998).

The complete lack of spatial variation in allele frequencies for collections of ocean-caught adult and juvenile *Acanthopagrus australis* from several estuaries suggests that this species effectively forms a single large panmictic population on Australia's east coast. Our data for ocean-caught adults alone could reflect the post-spawning migration and possible mixing of adults from genetically distinct estuary associated subpopulations (i.e. marine admixture). Species that display strong philopatry and consequent genetic subdivision of spawning aggregations often forage or migrate over vast distances before returning to natal

sites to spawn (e.g. Bowen et al. 2005). Thus, the limitation of our data set based on ocean-caught adults alone is that we are unable to distinguish between rangewide genetic homogeneity and marine admixture of a set of genetically distinct estuary associated subpopulations. However, the genetic homogeneity of juveniles provides more compelling evidence of the lack of any persistent genetic subdivision of populations that is attributable to an association with estuaries.

Our data are consistent with what is known of the breeding biology of *Acanthopagrus australis* and east coast oceanography, and suggest that both the southerly migration of adults and northerly dispersal of larvae via the EAC provide sufficient mixing to prevent rangewide population differentiation. The EAC is the major ocean current on the east coast. It produces a reliable, predominantly north–south flow of warm water originating in the tropics, but becomes progressively weaker and less reliable from ~33° S (central NSW), as the majority of the flow is deflected seaward in this area (Godfrey et al. 1980). Several authors have speculated on the EAC's effectiveness in transporting larvae to the far south coast of eastern Australia (Ayre 1990, Murray-Jones & Ayre 1997); however, genetic analysis of population differentiation has often revealed genetic homogeneity for widely separated collections of species with long-lived pelagic larvae. These include several species that are relatively immobile as adults because of habitat specialisation or attachment to, or within, benthic substrata (Banks et al. 2007, Curley & Gillings 2009). This homogeneity is most simply explained by a high degree of population connectivity that is maintained by dispersal of larvae within warm-core eddies of the EAC. Although the flow of the EAC is deflected seaward, eddies break off and continue to flow southwards, sometimes reaching the Bass Straight between Tasmania and the Australian mainland (40° S) (Nilsson & Cresswell 1981). The physical properties and southward penetration of these eddies vary greatly in space and time (Roughan & Middleton 2004), and have important implications for the growth, survival and transport of larvae. However, a recent survey of the frequency of occurrence and abundance of tropical (coral) reef fish in temperate subtidal rocky reef habitats in southern NSW highlighted the effectiveness of the warm-core eddies in affecting larval transport (Booth et al. 2007). The authors reported recurring recruitment of a diverse set of reef fish along the NSW coast, remarkably including recruitment at locations near the NSW/VIC state border (38° S), which is ~1700 km from the typical southern range limit of these fish on the Great Barrier Reef.

Evolutionary consequences of predicted change to the circulation pattern of the EAC

Eastern Australia is predicted to experience severe modification of major current flows due to climate change. Indeed, there are already reports of urchins (*Centrostephanus rodgersii*) being transported to the far south of their previous distributional range limit by the movement of larvae within warm-core eddies of the EAC (Banks et al. 2010), with adult populations now being established in Tasmania and having devastating effects on subtidal kelp forests and associated fauna (Johnson et al. 2005). For *Acanthopagrus australis*, range expansion may have little direct impact on its population structure, but could have serious implications for its estuary restricted congener, *A. butcheri*. *A. butcheri* is distributed within estuaries from southern NSW to Tasmania in the south, and Western Australia in the west. Our earlier works suggested that hybridisation and introgression involving *A. australis* have made a massive contribution to the genotypes of *A. butcheri* within NSW estuaries (Roberts et al. 2009, Roberts et al. 2010). A northerly range expansion by *A. australis*, facilitated by more frequent or further than usual northerly penetration of warm-core eddies could simply increase the size of this panmictic east coast population. Alternatively, the spread of *A. australis* may increase both the geographic range within which hybridisation occurs, and the number of hybrid-dominated lakes and lagoons. Indeed, our preliminary broad-scale genetic survey based on a small number of samples has already uncovered rare hybrids in Tasmanian estuaries (Roberts et al. 2009). Frequent easterly dispersal seems less likely for *A. australis* (although this is not impossible), as we now know that the 'southeast corner' of Australia is a major biogeographic barrier for several species that are regarded as 'good dispersers' (Waters et al. 2007, Ayre et al. 2009). The SE barrier region corresponds to a convergence zone of northerly flowing warm-core eddies of the EAC and cold waters of the westerly flowing Bass Straight Cascade. It therefore represents an area of extreme spatial variation in water temperature and salinity (images can be found at www.bom.gov.au) that presumably blocks along-shore dispersal of adults or transport of larvae. It now seems crucial to employ further genetic surveys of *Acanthopagrus* spp., beyond the recognised southern and western range limit of *A. australis* to determine baseline proportions of *A. australis* and/or their hybrids.

Acknowledgements. We thank the New South Wales Department of Primary Industries for collection permits; the Australian Research Council linkage and NSW Recreational Fishing Trust for grants to D.J.A., R. J. West and C. A. Gray; the

Institute for Conservation Biology of the University of Wollongong; R. J. West and C. A. Gray for advice and critical comments; and C. A. Gray and L. Bennet for provision of samples of juvenile fish. This is contribution 297 of the Ecological Genetics Group at the University of Wollongong.

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Editorial responsibility: John Choat, Townsville, Australia

Submitted: August 31, 2009; Accepted: May 24, 2010
Proofs received from author(s): July 28, 2010